Martin Brasier's contribution to the palaeobiology of the Ediacaran–Cambrian transition

ALEXANDER G. LIU[1], LATHA R. MENON[2], GRAHAM A. SHIELDS[3], RICHARD H. T. CALLOW[4] & DUNCAN MCILROY[5]

[1] *School of Earth Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, U.K.*
[2] *Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, Oxfordshire, OX1 3AN, U.K.*
[3] *Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, U.K.*
[4] *Statoil ASA, 4035 Stavanger, Norway.*
[5] *Department of Earth Sciences, Memorial University of Newfoundland, 300 Prince Philip Drive, St. John's, NL, A1B 3X5, Canada.*

Abstract

Martin Brasier's work spanned almost the entire geological column, but the origin of animals and the nature of the Cambrian Explosion were areas of particular interest. Martin adopted a holistic approach to the study of these topics that considered the interplay between multiple geological and biological phenomena, and sought to interpret the fossil record within the broad context of geological, biogeochemical, and ecological changes in the Earth system. Here we summarize Martin's main contributions in this area, and assess the impact of his findings on the development of this field.

> "*Karl Popper would have said that… palaeontology* [is] *not real science because you can't go out and sample it. I think absolutely the opposite. I think this is actually where science is. It's trying to guess what lies over the hill and map terra incognita. When people come in and colonize, that's just technology*."
>
> Martin Brasier, 2013
>
> (Excerpted from a phone interview with Robert Moor, *On Trails*, 2016)

Martin's path into the Ediacaran–Cambrian transition

Martin Brasier frequently articulated the story of his journey into the study of the Cambrian Explosion of animal life. Drawing comparisons to Darwin and Lyell, Martin observed that his research into the past also began by looking at the present – in his case, exploring Caribbean reefs and lagoons as a ship's naturalist on-board HMS Fawn and HMS Fox during his doctoral work in 1970 (Brasier 2009). Much of his early palaeontological research focused on Foraminifera (see Brasier 2012; Gooday in review), but these interests broadened to encompass other groups and ever more ancient organisms. During his time at the University of Reading, Martin was shown macrofossil specimens from the Ediacaran of Australia by Roland Goldring, which Martin later quipped he didn't study at the time because "[the Ediacara biota] *had been solved, Glaessner had worked it all out*". Martin did however take an interest in Roland's archaeocyathid sponges, which led him to Paris to work with Françoise Debrenne on the Cambrian Explosion.

Martin became fascinated by the conundrum of Darwin's Dilemma: the mystery of why animal fossils seemingly extended back in time only to the Cambrian Period when evolutionary theory predicted a much more ancient history for metazoan lineages. He saw the Cambrian Explosion as "*probably one of the strangest things that's ever happened to life on our planet*", and dedicated a significant amount of his career to attempting to resolve this problem. An early contribution to this area involved helping Michael House to organize one of the first symposia on the Cambrian Explosion, for the Systematics Association in 1978. Meanwhile, work at the University of Hull explored the ecology and taphonomy of archaeocyaths and the "Tommotian" trace fossils and skeletal biota of Nuneaton: the Small Shelly Fossils, or "*small smelly fossils*" as Martin fondly referred to them (Brasier 1976, 1984, 1986; Brasier *et al.* 1978; Brasier & Hewitt 1979). Those studies later expanded to encompass the broader Cambrian Explosion, and particularly its global palaeoenvironmental context (Brasier 1982, 1985).

Following his move to the University of Oxford in 1988, Martin became focused on the interrelationship between the evolution of animal life, nutrient flux, and the global ocean-atmosphere system, as evidenced by authigenic minerals and geochemistry (e.g. Brasier 1990, 1991, 1992; Brasier *et al.* 1990; Brasier *et al.* 1992). His arrival in Oxford coincided with a surge in interest in carbon isotope perturbations around the Ediacaran–Cambrian boundary (Hsu *et al.* 1985; Knoll *et al.* 1986; Magaritz *et al.* 1986; Tucker 1986). With a

stable isotope laboratory at his disposal, Martin became an isotope enthusiast, launching a series of chemostratigraphic studies through the 1990's, spurred on by a healthy rivalry with the competing Harvard group (e.g. Knoll *et al.* 1995). His interest in isotopes refined stable isotope stratigraphy across the Ediacaran–Cambrian boundary, culminating, through his involvement in the International Subcommission on Cambrian Stratigraphy, with an internationally agreed definition for the basal Cambrian boundary (Brasier *et al.* 1994a; Landing & Geyer this volume). By the end of the decade, Martin had fully incorporated global isotopic trends into a holistic synthesis of the Ediacaran–Cambrian transition (Brasier & Lindsay 2001) that had its roots 20 years earlier (Brasier 1980, 1982).

Between 1992 and 1995, Martin supervised his first student on the Ediacaran–Cambrian transition, Duncan McIlroy, and it was at this time that Martin was partly drawn away from the carbonate-rich Cambrian successions and towards the fossiliferous siliciclastic Ediacaran–Cambrian sections of Avalonia and Baltica (Brasier & McIlroy 1998; McIlroy *et al.* 1998). It was not until the early 2000s that Martin truly engaged with the Ediacaran during a visit to Mistaken Point with Guy Narbonne of Queens University. Following McIlroy's move to Memorial University of Newfoundland (Canada), Martin became an adjunct professor at Memorial University, and from 2005 onwards he visited Newfoundland with graduate students for several weeks each year (Fig. 1) until his death. Many of these students, including Jonathan Antcliffe, Richard Callow, Alex Liu, Latha Menon, Jack Matthews and Renee Hoekzema, continue to explore aspects of Ediacaran geology and palaeobiology in Newfoundland and elsewhere. Although Martin extended his research ever further back in time, "*working on ever older and more puzzling rocks – as I myself grew more ancient and puzzled*" (see Antcliffe *et al.* this volume), the question of animal origins, and the enigma of the Cambrian Explosion, remained a core area of his studies. Some of the highlights of his Ediacaran and Cambrian work, and their intellectual impact on the field, are outlined below.

Refining stratigraphic understanding

Martin's work, particularly in the 1980s and 1990s, had a strong focus on refining Ediacaran–Cambrian stratigraphy in order to develop a global framework upon which to pin geological and evolutionary events. He noted at his retirement event in 2014 that "*although everybody is interested in the biology of the Cambrian Explosion, actually defining the terms and the nature of rocks across that time was a fundamental part of developing the language we*

needed…". As part of his formal Reply upon receiving the Lyell Medal of the Geological Society that same year, he noted: "*It took twenty years (1973–1993) to help settle a definition of the Precambrian–Cambrian boundary, and another two decades to help characterize the new Ediacaran System*".

Martin's involvement in this important work utilized several independent records, across multiple continents. Following early work on the Cambrian boundary sections in India (Brasier & Singh 1987), he proceeded to integrate geochemical and biostratigraphic records from places as far afield as Scotland, Iran, Oman, China, Mongolia, Spain and Australia, demonstrating thereby major discontinuities in classic GSSP candidate sections (Brasier *et al.* 1979; Brasier, *et al.* 1990; Brasier *et al.* 1996; Shields *et al.* 1997; Brasier & Shields 2000; Lindsay *et al.* 2005). These studies contributed to an increasingly robust understanding of temporal changes in geochemical records during the Ediacaran–Cambrian transition, and also include some of the first publications to recognise overlaps in the biostratigraphic ranges of key Cambrian biotas (e.g. Brasier *et al*. 1979). Although he was not a geochronologist, Martin became associated with several projects involved in dating significant Ediacaran and Cambrian sections worldwide, including studies of material from Oman (Brasier *et al.* 2000), and most recently efforts to date the fossiliferous Ediacaran localities in Newfoundland.

Martin became involved in global discussions regarding Cambrian stratigraphic correlation during the late 1980s and early 1990s, holding positions as Secretary of the Working Group on the Precambrian–Cambrian boundary, and leader of IGCP Project 303 on Precambrian–Cambrian event stratigraphy (Brasier *et al*. 1994b). Most notably, in his role as President of the International Subcommission on Cambrian Stratigraphy (1992–1996) Martin presided over the key decision regarding the placement of the Global Stratotype Section and Point for the base of the Cambrian System. This process required considerable diplomacy, with multiple nations competing for the GSSP (Brasier *et al.* 1994a; Brasier 2009). The eventual GSSP section, at Fortune Head in Newfoundland, was chosen partly on the basis of its possession of the first appearance datum of the *Treptichnus pedum* (formerly *Phycodes pedum*) trace fossil assemblage (summarized in Brasier *et al.* 1994a; McIlroy & Brasier this volume). Although this decision has largely withstood the test of time, refinement of formal stratigraphy in both the Cambrian and the Neoproterozoic are ongoing (e.g. Narbonne *et al*. 2012; Shields-Zhou *et al*. 2012; Landing *et al*. 2013; Babcock *et al.* 2014; Geyer & Landing this volume). Martin retained an active role in Subcommission activities, and was a Voting

Member of the International Subcommission on Ediacaran Stratigraphy at the time of his death.

Decoding the Ediacaran biota

Martin worked on several different groups of Cambrian and Neoproterozoic organisms, but perhaps the most challenging (and ultimately rewarding) group were the Ediacaran soft-bodied macrobiota. To the uninitiated, study of the Ediacaran macrobiota appears a daunting task: many of the fossils bear little or no resemblance to any extinct or extant taxon, and their paucity of recognisable morphological characters has contributed to significant uncertainty regarding their position in the eukaryotic tree. Martin conducted fieldwork in locations including Canada, Oman, Namibia and Brazil to attempt to resolve the question of what the Ediacaran organisms were. The consensus opinion when Martin began his Ediacaran–Cambrian research was that many of the Ediacaran macro-organisms were animals (cf. Glaessner 1984), but following Seilacher's famous suggestion of an alternative Vendobiont hypothesis (Seilacher 1984, 1989), considerable debate and uncertainty has surrounded their phylogenetic position. Martin was keen to emphasize that the Precambrian world was different, and that the principle of uniformitarianism could not be extrapolated back into the Precambrian as reliably as it could in the Phanerozoic: "*the world before the Cambrian was, arguably, more like a distant planet*" (Brasier 2009). He also recognized that 'shoehorning' Ediacaran fossils into modern groups was unwise, since many characters diagnostic of extant crown groups were likely to have developed in response to extrinsic events or factors that had not yet come to pass in the Ediacaran. In particular, he was in recent years a vocal advocate of questioning the assumption that many Ediacaran macro-organisms were metazoan, critically assessing the evidence, promoting consideration of the null hypothesis, and encouraging debate and discussion (e.g. Antcliffe *et al*. 2014). Where the evidence weighed against the null hypothesis, however, he remained open to the possibility that some Ediacaran forms might represent simple animals (e.g. Liu *et al*. 2015b).

Although he participated in field trips to Ediacaran localities from the 1970s onwards, it was only in the early 2000s that Martin started to seriously examine Ediacaran macrofossils, with his first foray in this field being a Masters student project on *Charnia masoni* (completed by Jo Slack). This led to over a decade of research into the Ediacaran macrobiota, which coincided with a significant global invigoration of the field. Perhaps

unsurprisingly, this work also included occasional descriptions of microfossils (e.g. Zhou *et al.* 2001).

Consideration of growth and development

Martin's approach to investigating Ediacaran macro-organisms was to focus on a small number of iconic, representative taxa; to study these in detail; and to assess their growth and development in order to attempt to constrain their phylogenetic position (an approach outlined in Brasier & Antcliffe 2004). Work undertaken with Jonathan Antcliffe on *Charnia* demonstrated how its mode of growth seemingly differs from that of extant sea pens, thus permitting a pennatulacean affinity for *Charnia* to be refuted (Antcliffe & Brasier 2007a, 2008). Similar studies into *Dickinsonia* (Brasier & Antcliffe 2008; utilising specimens from the Goldring collection) and *Palaeopascichnus* (Antcliffe *et al.* 2011) provided further contributions to our knowledge of those taxa and their construction, and expanded the armoury of approaches used to examine Ediacaran macrofossils. The influence of this work can be clearly seen in recent studies into the growth, development and morphogenesis of Ediacaran macrofossils (e.g. Hoyal Cuthill & Conway Morris, 2014; Gold *et al*. 2015). Martin's studies also introduced a technological innovation to Ediacaran palaeobiology: the laser scanning of fossil-bearing surfaces (Fig. 2; Antcliffe & Brasier 2011). Laser scanning permits fine-scale quantitative studies of morphology, and reveals morphological characters that cannot be easily observed in the field.

Consideration of other Ediacaran frondose taxa (e.g. *Bradgatia* and *Charniodiscus*) explored how those organisms might be related to one another (Brasier & Antcliffe 2004, 2009), how disparate their morphologies could be (Antcliffe & Brasier 2007b) and the details of their architecture and taxonomy, culminating in the development of a coherent system with which to describe and classify rangeomorph organisms (Brasier *et al.* 2012). That latter publication provided a testable framework in which to explore frondose taxa, and has stimulated ongoing research into the fundamental question of what constitutes ecophenotypic versus genotypic variability in Ediacaran populations (e.g. Wilby *et al.* 2015; Liu *et al.* 2016). Though he did not describe significant numbers of new Ediacaran macrofossil taxa, Martin was particularly proud of deciphering *Beothukis mistakensis* (Brasier & Antcliffe 2009), which he considered to be a 'Rosetta Stone' for the understanding of rangeomorphs. As with the other taxa he named from Newfoundland (e.g. *Vinlandia*, Brasier *et al.* 2012), Martin

191 favoured names that celebrated the history of the island and the language of its indigenous
192 populations.

193

194 *A focus on Avalonia*

195 Martin's work included descriptions of Ediacaran fossils from Australia (Brasier & Antcliffe
196 2008), Iran (Menon *et al*. In Prep), Brazil (Parry *et al*. In Prep) and Siberia (Liu *et al.* 2013),
197 but much of his Ediacaran research was undertaken on sites either in England, or in
198 Newfoundland. The classic English localities of the Long Mynd and Charnwood Forest,
199 along with the coastal sections of Newfoundland, all lay on the margins of the microcontinent
200 of Avalonia during late Ediacaran times (Cocks *et al.* 1997). As such, they exhibit many
201 similarities in age, facies and fossil assemblage (Wilby *et al.* 2011; Noble *et al.* 2015), and in
202 the past decade Martin made a concerted effort to better understand these regions and their
203 relationship to wider global patterns and processes.

204

205 *Charnwood Forest*

206 The Ediacaran–Cambrian inlier of Charnwood Forest in Leicestershire, central England, was
207 for Martin a classic place to take new students due to its accessibility, its historical
208 importance in Ediacaran palaeontology, and because it is not a very easy area to understand
209 without geological mapping and careful fieldwork. The art of deciphering stratigraphy and
210 palaeoenvironment is something that Martin always loved, be it mapping the location of
211 Precambrian cherts (e.g. Wacey *et al*. 2010) or working out field relations between dated
212 igneous rocks and Ediacaran successions to indirectly constrain the age of the Ediacaran biota
213 (McIlroy *et al.* 1998).

214 The Charnian successions became a central focus of Martin's research following his
215 2005 visit to Mistaken Point in Newfoundland, during which time his Oxford group first
216 started to develop ideas pertaining to growth and morphology of the Ediacaran macro-
217 organisms. The easy accessibility of type material of *Charnia masoni* and *Bradgatia*
218 *linfordensis* allowed Martin to employ his skills as an artist to create sketches that were more
219 informative than any individual photograph. Martin used a technique where he drew the
220 same fossil multiple times using illumination from different directions to build up a picture of

the specimen that was simultaneously lit from several directions (Fig. 3). Although he called it '*camera lucida*', in truth it often involved him tracing over images directly on his computer monitor. While drawing the type material of *Charniodiscus*, Martin suggested that it might actually be composed of several fronds orientated at angles to one another and compressed into the same plane (unpublished work discussed widely at conferences; Fig. 3; contrast this with Brasier & Antcliffe 2009, fig. 12), which, if correct, potentially has implications for all the other currently valid species of *Charniodiscus* (*C. arboreus, C. longus, C. oppositus, C. procerus, C. spinosus* and *C. yorgensis*), which appear to only have one frond and as such would have to be transferred to another genus. *Charniodiscus* is a particularly problematic taxon, and although progress is being made in understanding its morphology (e.g. Ivantsov 2016), it remains to be seen whether Martin's interpretation is correct. Much of Martin's work on rangeomorphs utilized material from Charnwood, and he also contributed to discussions regarding protection of the Charnwood localities in his role as a member of the *Charnia* Research Group.

The Long Mynd, Shropshire

The other main English Ediacaran sections are to be found on the Long Mynd of Shropshire. The purported macrofossils from this area were first described by John Salter (Salter 1856, 1857) who was a contemporary of Charles Darwin, and the material from the Long Mynd was posited by Darwin as a partial solution to the unexpectedly sudden appearance of fossils at the base of what we now call the Cambrian Explosion (Darwin 1859). Martin had been fond of relating the sad story of John Salter, who was from a relatively humble background and had worked his way up to be a palaeontologist for the British Geological Survey, only to be sacked just before reaching pensionable age. Struggling to support his family, and suffering from bouts of depression, he finally committed suicide (Callow *et al.* 2011). In the course of Martin's revisiting of the Longmyndian fossils, the wonderful Darwin Correspondence Project (e.g. Burkhardt & Smith 1985) provided a more complete story of Salter's last years, which lends support to the idea that he suffered from what we would now call bipolar disorder (Callow *et al.* 2011). Salter's tragic story, especially the way that his work was overlooked and side-lined, touched Martin, who took delight in bringing Salter's work to a modern audience within the context of historical geology.

The key scientific questions regarding the Longmyndian relate to what its dominantly discoidal fossil assemblage represents, and how the shallow-marine to fluvial depositional environments relate to the largely marine sections seen elsewhere in Avalonia. The various discoidal structures of the Long Mynd have been the subject of much discussion in the geological literature (summarised in Callow & Brasier 2009a; Callow *et al.* 2011). Debate had surrounded the biogenicity of the small, circular impressions from the Burway, Synalds and Lightspout formations, with interpretations ranging from gas escape structures or raindrops to body and trace fossils of Ediacaran macro-organisms (e.g. Cobbold 1900; McIlroy *et al.* 2005; Toghill 2006). Martin's own investigations in the Long Mynd led to expanded descriptions of microfossils (originally described by Timofeyev *et al.* 1980, and Peat 1984), and the recognition that they could be preserved in multiple taphonomic styles (Callow & Brasier 2009b). Follow-up work with Latha Menon investigated the problem of what the discoidal structures actually represent by utilising serial grinding techniques to digitally reconstruct their three-dimensional morphology. This work revealed that the Longmyndian discoidal impressions were formed by the interaction of escaping fluids within finely laminated, microbial-mat-bound sediments (Menon *et al.* 2016; Menon *et al.* this volume), finally establishing that they arose from a combination of abiogenic processes and the presence of microbial mats.

So from a position where Martin felt that the Longmyndian sections were key to understanding evolution in the latest Ediacaran (his Kotlin Crisis; Brasier 1995), gradually, taxon by taxon, detailed objective work has reduced us to a position where there are no longer any authentic Ediacaran macrofossils reported from the Long Mynd (though that is not to say his Kotlin Crisis has been abandoned; see for example Kolesnikov *et al*. 2015). John Salter's novel assertion that there was Precambrian animal life is correct (Salter 1856), but sadly not based on the material he knew. The critical reassessment of the discoidal forms of the Long Mynd owe much to Martin instilling into his students the importance of constant vigilance in interpreting ancient markings, and his emphasis on the importance of the null hypothesis. In this case, the influence of microbial mats on fluid-filled sediments, driving millimetre-scale fluid escape, and affecting their surface expression, was entirely sufficient to explain the range of discoidal markings found on the Long Mynd. This work also expanded the range of influence of microbial mats on Ediacaran sediments, and highlighted the need to recognize the key role of microbes when examining the fossil record - a subject close to Martin's heart (e.g. Callow & Brasier 2009a; Brasier *et al.* 2010).

Meanwhile Martin's interests in determining the origin of the Long Mynd's other enigmatic surface impression, Arumberia (Bland 1984; McIlroy & Walter 1997; McIlroy *et al.* 2005; Kolesnikov *et al*. 2012), and in refining the geochronological record of the locality, are ongoing areas of research for his group. He passed away before embarking on the next phase of our Longmyndian investigations—an opportunity to compare the sections to thick non-marine Ediacaran successions in Newfoundland—but he would have been amused to note that, as in all known non-marine Ediacaran successions, there is currently no evidence for the classic Ediacaran macrobiota. Had the Ediacaran biota truly been composed of lichens (Retallack 1994), environments like this are surely amongst the most likely places where we would have expected to find them.

Newfoundland, Canada

In addition to the work on rangeomorphs mentioned previously, Martin supported the exploration of sites in Newfoundland by his students. Research into Ediacaran taphonomy, largely using data collected from Newfoundland, offered a comprehensive assessment of how taphonomic processes and styles changed across the Ediacaran–Cambrian boundary, and their impact on our interpretation of the fossil record (Callow & Brasier 2009a). Martin also contributed to the recognition that some impressions on Ediacaran fossil-bearing surfaces previously described as valid taxa (e.g. *Ivesheadia, Shepshedia* and *Blackbrookia*; Boynton & Ford 1995) instead reflect decayed carcasses of other Ediacaran organisms (Liu *et al.* 2011; though see Laflamme *et al.* 2011; Wilby, *et al.* 2011). The recognition that time averaging occurs on Ediacaran bedding planes was a revolutionary idea at the time, and has been built upon by several other studies recognising the presence of multiple successive communities preserved on individual Ediacaran bedding planes (e.g. Antcliffe *et al.* 2015; Wilby *et al.* 2015). It has also inspired studies into the potential ecological impact of the appearance (and post-mortem influence) of macroscopic soft-bodied organisms on both benthic communities and the late Ediacaran carbon cycle (e.g. Liu *et al*. 2015a; Budd & Jensen 2015; Dufour & McIlroy this volume).

Martin and his students have also made significant contributions to the Ediacaran ichnofossil record. The description and interpretation of 565 Ma horizontal surface trails in the Mistaken Point Formation of Newfoundland (Liu *et al.* 2010a; Liu *et al.* 2014a), and of ~560 Ma vertical equilibration traces in the Fermeuse Formation (Menon *et al.* 2013), extend

the record of metazoan movement considerably into the Ediacaran Period. Those discoveries provided a search image for Ediacaran researchers that appears to have stimulated a considerable increase in the recognition of late Ediacaran trace fossils worldwide (e.g. Chen *et al.* 2013; Carbone & Narbonne 2014; Macdonald *et al.* 2014; see Liu & McIlroy 2015), providing some of the strongest existing evidence for the presence of motile metazoans among the largely sessile Ediacaran macro-organisms. However, Martin was wary of accepting all claims for complex metazoan movement or feeding, staying true to his belief that the null hypothesis must first be rejected before considering more ground-breaking claims (Brasier 2015). He was involved in questioning both 'grazing' traces of *Dickinsonia*-like organisms (McIlroy *et al.* 2009), and claims for bioturbation in Siberian rocks (Brasier *et al.* 2013a). These challenges were nevertheless constructive, and were intended to spur debate that will ultimately resolve the nature of these important materials.

Martin oversaw the description of discoveries of communities of juvenile rangeomorphs within the Mistaken Point Ecological Reserve (Liu *et al.* 2012), and personally discovered the holotype of what would come to be known as *Haootia quadriformis* (Liu *et al.* 2014b) on the Bonavista Peninsula. This remarkable fossil caused a lot of head-scratching and beard-stroking, but upon discovery of a second specimen in 2013, an interpretation of *Haootia* as recording an organism with fibrous musculature was developed (Liu *et al.* 2014b, 2015b). Once again, Martin was keen to ensure that the null hypothesis was first rejected before he would seriously consider options that implied the presence of metazoan musculature, and even after publication he was careful to stress that this interpretation was a "*tentative reconstruction*", made on the basis of available evidence. His demand for high standards continued throughout his Ediacaran research, for example in his questioning of the terrestrial interpretation of the Ediacaran biota (e.g. Retallack 2010, 2013). He considered such interpretations to require special pleading to reinterpret sections that, on process-based physical sedimentological evidence, have always been considered marine (e.g. Liu *et al.* 2010b; Callow *et al.* 2013).

Palaeoenvironmental and preservational context was central to Martin's approach to fieldwork, and he would encourage his students to visualize fossil assemblages in their original depositional environments, expertly producing impromptu sketches of possible scenarios in his notebook after meticulously recording his field observations (e.g. Fig. 4). This broad consideration of palaeoenvironment and context formed an important counterpoint to the detailed study of individual Ediacaran fossils. His work on both was driven by a

combination of detailed observation, imagination, and biological insight, guided and tempered by his wide experience. An example of his rapid assimilation and interpretation of new observations is given by the reinterpretation of the remarkable preservation of Ediacaran rangeomorphs at Spaniard's Bay (Brasier *et al.* 2013b). An observation by one of his students that the basal discs of fronds preserved on this surface show a steep undercutting on one side struck him immediately as of significance, and led to his proposing a hydraulic model, which the group tested and confirmed with sedimentological and morphological evidence. This reassessment of the context of preservation has important implications for the interpretation of morphological features in Ediacaran rangeomorphs (e.g. compare discussions in Brasier *et al.* 2013b with those in Narbonne *et al.* 2009). In addition to studying the fossils and their sedimentological context, Martin, along with Duncan McIlroy and Jonathan Antcliffe, had in recent years developed hypotheses regarding the role of geochemical cycling in Ediacaran ecosystems (Dufour & McIlroy this volume). These hypotheses are currently being tested through the application of NanoSIMS to investigate sulfur cycling, in collaboration with David Wacey, using material from Newfoundland in particular. This line of research was in its infancy at the time of Martin's death, but had begun to yield preliminary results by demonstrating the biogenic origin (via microbial sulfate reduction) of pyrite framboids within mineralized veneers at macrofossil-bearing interfaces (Wacey *et al.* 2015; see also Liu 2016). Further sulfur isotope data will be published in the coming years as this avenue of research is explored in greater detail.

Martin's work in Newfoundland led to his being invited along with Alex Liu to write the Global Comparative Analysis of Ediacaran Fossil Sites for the Government of Newfoundland and Labrador: a document that in 2015 was submitted to UNESCO as part of the Canadian nomination of Mistaken Point Ecological Reserve for World Heritage Site status (Liu & Brasier 2012). As well as comparing Ediacaran fossil sites worldwide against a number of palaeontological criteria, the report set out a protocol for the assessment of the Outstanding Universal Value of Precambrian fossil sites, which Martin hoped would make a lasting contribution to society's appreciation of important palaeontological localities worldwide.

Considering the interplay between Earth and Life

Core to Martin's thinking when assessing Ediacaran and Cambrian evolutionary events was the interplay between evolution and the wider biosphere. He realized that the patterns revealed in the fossil record could only be deciphered through consideration of the contemporaneous geological and geochemical events that triggered, or were consequences of, evolutionary innovations. His deep musing on approaches to interpreting the fossil record, which he regarded as akin to playing a card game without knowing the rules (see Antcliffe *et al.* this volume), was reflected in his public lectures and nicely summarised in his popular science book on the subject, *Darwin's Lost World* (Brasier 2009). In this book, intended to inspire new generations of students as well as the general reader, he highlighted the dramatic impact of the evolutionary innovation of predation among early animals, driving an arms race of attack and defence mechanisms and culminating in the "circus of worms"—the sudden appearance of widespread and deep burrowing—that so strikingly characterizes the transition from the Ediacaran to Cambrian (Herringshaw *et al*. this volume; McIlroy & Brasier this volume). His perspective was profoundly influenced by an Earth Systems view, involving feedbacks, symbiotic associations, and the possibilities of catastrophic collapses of interconnected webs resulting from subtle internal as well as external factors. These ideas, many of which stem from observations made during his time as a ship's naturalist, fed even more strongly into his second book, about the origins of complex life, *Secret Chambers* (Brasier 2012).

The forcing factors for animal evolution and the Cambrian Explosion

A particularly long-running strand of Martin's research was his investigation of whether the Cambrian Explosion was a real event, and what may have triggered it. Over two decades, Martin continually refined his ideas towards a sophisticated synthesis of intricately interconnected phenomena, which together provided the environmental context for the evolutionary diversification of animals. Some of his earliest work investigated the role of sea level change and facies variations in driving the Cambrian Explosion (Brasier 1982). Extensive erosion continues to be explored as a tenable trigger for the Cambrian radiation (e.g. Peters & Gaines 2012). Martin later considered the impact of factors such as climate change, carbon cycle instability, eutrophication and anoxia (Brasier 1991, 1992), and even supercontinent amalgamation (Brasier & Lindsay 2001), the latter in part informed by his previous work collating the distribution of fossils and facies in several regions to assist in the

assembly of widely cited Neoproterozoic to Palaeozoic palaeogeographic reconstructions (McKerrow *et al*. 1992; Torsvik *et al*. 1996). The occurrence of a broad belt of glauconite and phosphate-rich sedimentary facies in the Early Cambrian was a long-lasting source of inspiration and intrigue (Brasier 1980, 1992; Brasier & Callow, 2007), and Martin's favourite question for speakers on Ediacaran–Cambrian topics at conferences was "*but what about the phosphate?*", a question he argued could be asked with justification of any researcher of this interval. Martin's observations of the apparent onset of phosphatization at shallow depths within the sediment profile led him to invoke nutrients such as phosphate as a potential trigger for the Cambrian Explosion and the advent of biomineralization (Brasier 1980, 1990, 1992). Whether phosphate deposition was a cause (Brasier 1992) or a consequence (e.g. Butterfield 2003) of the Cambrian radiation has yet to be resolved, but Martin undoubtedly caused many to ponder the fundamental importance of nutrients for evolution (e.g. Tucker, 1992; Boyle *et al.* 2014). Resolving the role of phosphate in fossilization (Brasier 1984, 1985, 1990) and oxygenation (Brasier & Callow 2007) became another long-running theme of Martin's research, and was used as a primary example of his hypothesis that the nature of the fossil record has changed through time (cf. Callow & Brasier 2009a; Brasier *et al.* 2011). He recognised that soft-bodied forms are preserved by phosphate in exquisite detail from the Early Cambrian to the late Mesoproterozoic, and suggested that the quality of the fossil record (somewhat paradoxically) improves the further back in time we go (Brasier 2009).

Going forward

At the time of his death, Martin's research into the Ediacaran–Cambrian transition was far from over, and there remains much to do to understand evolutionary events and processes during this interval. We have touched upon several of the ways in which studies Martin was involved in are already being built upon (e.g. Dufour & McIlroy this volume). However, Martin's greatest legacies in this field are arguably his involvement in defining the Ediacaran–Cambrian boundary (and also the basal Ediacaran GSSP in his role as a voting member of the Ediacaran Subcommission), and his support and expansion of the Ediacaran scientific community, both through the guidance of members of his own group, and the encouragement he offered, both informally and in reviews, to many scientists around the world seeking to tackle Ediacaran–Cambrian problems.

Martin's work questioned several of the hypotheses that were 'in vogue' at the time, for example the severity of Neoproterozoic Snowball Earth events (Leather *et al.* 2002; Allen *et al.* 2004; Kilner *et al.* 2005). Importantly, in the best scientific tradition, he was not above questioning his own previous interpretations, for example revoking specimens he had earlier described as peristaltic burrowing (Brasier & McIlroy 1998; then see Brasier & Shields 2000) and the oldest sponge spicules (Brasier *et al.* 1997; then see Antcliffe *et al.* 2014). In much the same way as his approach to palaeobiology in general, Martin's Ediacaran–Cambrian work challenged existing paradigms, expanded knowledge via application of new techniques to known sections, and provided novel hypotheses for critical testing. His studies throughout his career were rigorous, vigorous, thought-provoking, and scholarly. They often combined strong fieldwork elements in order to provide essential context for palaeontological material with the development of theoretical frameworks through which to make sense of the unusual organisms and events. This approach is something that many of his former students are keen to uphold. At its core, Martin's Ediacaran–Cambrian work was focused on pushing the boundaries of knowledge: "*trying to guess what lies over the hill and map terra incognita*", and ultimately understand the questions of how and why animals evolved. He may not have answered those questions completely, but he certainly played a prominent role in steering the scientific community towards the solutions.

Acknowledgments

We thank Palaeocast for making public their recordings of Martin's Lyell Lecture at his retirement event at the University of Oxford in September 2014, from which several of the quotes in this article were taken, and the Geological Society of London, whose website records Martin's formal Reply upon receiving the Lyell Medal in 2014. Simon Harris of the British Geological Survey provided an image for Figure 3a, and Per Ahlberg kindly provided information on Martin's Cambrian Subcommission activities.

References

ALLEN, P.A., LEATHER, J. & BRASIER, M.D. 2004. The Neoproterozoic Fiq glaciation and its aftermath, Huqf supergroup of Oman. *Basin Research*, **16**, 507-534.

ANTCLIFFE, J.B. & BRASIER, M.D. 2007a. *Charnia* and sea pens are poles apart. *Journal of the Geological Society, London*, **164**, 49-51.

ANTCLIFFE, J.B. & BRASIER, M.D. 2007b. Towards a morphospace for the Ediacara biota. *In:* VICKERS-RICH, P. & KOMAROWER, P. (eds) *The Rise and Fall of the Ediacaran Biota*. Geological Society, London, Special Publications, **286**, 377-386.

ANTCLIFFE, J.B. & BRASIER, M.D. 2008. *Charnia* at 50: Developmental models for Ediacaran fronds. *Palaeontology*, **51**, 11-26.

ANTCLIFFE, J.B. & BRASIER, M.D. 2011. Fossils with little relief: Using lasers to conserve, image, and analyze the Ediacara biota. *In:* LAFLAMME, M., SCHIFFBAUER, J.D. & DORNBOS, S.Q. (eds) *Quantifying the Evolution of Early Life*. Topics in Geobiology, Springer Science and Business Media B.V., **9,** 223-240.

ANTCLIFFE, J.B., BRASIER, M.D. & GOODAY, A. 2011. Testing the protozoan hypothesis for Ediacaran fossils: developmental analysis of *Palaeopascichnus*. *Palaeontology*, **54**, 1157-1175.

ANTCLIFFE, J.B., CALLOW, R.H. & BRASIER, M.D. 2014. Giving the early fossil record of sponges a squeeze. *Biological Reviews of the Cambridge Philosophical Society*, **89**, 972-1004.

ANTCLIFFE, J.B., HANCY, A.D. & BRASIER, M.D. 2015. A new ecological model for the ~565Ma Ediacaran biota of Mistaken Point, Newfoundland. *Precambrian Research*, **268**, 227-242.

ANTCLIFFE, J.B., MCILROY, D., LIU, A.G., WACEY, D., MENON, L.R. & MCLOUGLIN, N. THIS VOLUME. How Martin Brasier changed the way we think about the fossil record. *In*: BRASIER A.T., MCILROY, D. & MCLOUGHLIN, N. (eds) *Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier.* Geological Society of London, Special Publication ****, **-**.**

BABCOCK, L.E., PENG, S., ZHU, M., XIAO, S. & AHLBERG, P. 2014. Proposed reassessment of the Cambrian GSSP. *Journal of African Earth Sciences*, **98**, 3-10.

BLAND, B.H. 1984. *Arumberia* Glaessner & Walter, a review of its potential for correlation in the region of the Precambrian–Cambrian boundary. *Geological Magazine*, **121**, 625-633.

BOYLE, R., DAHL, T.W., DALE, A.W., SHIELDS-ZHOU, G., ZHU, M.-Y., BRASIER, M.D., CANFIELD, D.E. & LENTON, T. 2014. Stabilization of the coupled oxygen and phosphorus cycles by the evolution of bioturbation. *Nature Geoscience*, **7**, 671-676.

BOYNTON, H.E. & FORD, T.D. 1995. Ediacaran fossils from the Precambrian (Charnian Supergroup) of Charnwood Forest, Leicestershire, England. *Mercian Geologist*, **13**, 165-182.

BRASIER, M.D. 1976. Early Cambrian intergrowths of archaeocyathids, *Renalcis*, and pseudostromatolites from South Australia. *Palaeontology*, **19**, 223-245.

BRASIER, M.D. 1980. The Lower Cambrian transgression and glauconite-phosphate facies in western Europe. *Journal of the Geological Society, London*, **137**, 695-703.

BRASIER, M.D. 1982. Sea-level changes, facies changes and the Late Precambrian—Early Cambrian evolutionary explosion. *Precambrian Research*, **17**, 105-123.

BRASIER, M.D. 1984. Microfossils and small shelly fossils from the lower Cambrian *Hyolithes* limestone at Nuneaton, English Midlands. *Geological Magazine*, **121**, 229-253.

BRASIER, M.D. 1985. Evolutionary and geological events across the Precambrian–Cambrian boundary. *Geology Today*, **1**, 141-146.

BRASIER, M.D. 1986. The succession of small shelly fossils (especially conoidal microfossils) from English Precambrian–Cambrian boundary beds. *Geological Magazine*, **123**, 237-256.

BRASIER, M.D. 1990. Phosphogenic events and skeletal preservation across the Precambrian-Cambrian boundary interval. *Geological Society, London, Special Publications*, **52**, 289-303.

BRASIER, M.D. 1991. Nutrient flux and the evolutionary explosion across the Precambrian-Cambrian boundary interval. *Historical Biology*, **5**, 85-93.

BRASIER, M.D. 1992. Nutrient-enriched waters and the early skeletal fossil record. *Journal of the Geological Society*, **149**, 621-629.

BRASIER, M.D. 1995. The basal Cambrian transition and Cambrian bio-events (from Terminal Proterozoic extinctions to Cambrian biomeres). *In:* WALLISER, O.H. (ed.) *Global Events and Event Stratigraphy*. Springer Verlag, Berlin, 113-138.

BRASIER, M.D. 2009. *Darwin's Lost World. The Hidden History of Animal Life*. Oxford University Press, Oxford, 304 pp.

BRASIER, M.D. 2012. *Secret Chambers: the Inside Story of Cells and Complex Life*. Oxford University Press, Oxford, 305 pp.

BRASIER, M.D. 2015. Deep questions about the nature of early-life signals: a commentary on Lister (1673)'A description of certain stones figured like plants'. *Philosophical*

Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences, **373**, 20140254.

BRASIER, M.D. & ANTCLIFFE, J.B. 2004. Decoding the Ediacaran enigma. *Science*, **305**, 1115-1117.

BRASIER, M.D. & ANTCLIFFE, J.B. 2008. *Dickinsonia* from Ediacara: A new look at morphology and body construction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 311-323.

BRASIER, M.D. & ANTCLIFFE, J.B. 2009. Evolutionary relationships within the Avalonian Ediacara biota: new insights from laser analysis. *Journal of the Geological Society, London*, **166**, 363-384.

BRASIER, M.D. & CALLOW, R.H.T. 2007. Changes in the patterns of phosphatic preservation across the Proterozoic-Cambrian transition. *Memoirs of the Association of Australasian Palaeontologists*, **34**, 377-389.

BRASIER, M.D. & HEWITT, R.A. 1979. Environmental setting of fossiliferous rocks from the uppermost Proterozoic—Lower Cambrian of central England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **27**, 35-57.

BRASIER, M.D. & LINDSAY, J.F. 2001. Did supercontinent amalgamation trigger the Cambrian Explosion? 69-89. *In:* ZHURAVLEV, A.Yu and RIDING, R. (eds) *The Ecology of the Cambrian Radiation.* Perspectives in Palaeobiology and Earth History. Columbia University Press, New York.

BRASIER, M.D. & MCILROY, D. 1998. *Neonereites uniserialis* from c.600Ma year old rocks in western Scotland and the emergence of animals. *Journal of the Geological Society, London*, **155**, 5-12.

BRASIER, M.D. & MCILROY, D. THIS VOLUME. Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northen Norway. *In*: BRASIER A.T., MCILROY, D. & MCLOUGHLIN, N. (eds) *Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier.* Geological Society of London, Special Publication **, **-**.

BRASIER, M.D. & SHIELDS, G. 2000. Neoproterozoic chemostratigraphy and correlation of the Port Askaig glaciation, Dalradian Supergroup of Scotland. *Journal of the Geological Society*, **157**, 909-914.

BRASIER, M.D. & SINGH, P. 1987. Microfossils and Precambrian–Cambrian boundary stratigraphy at Maldeota, Lesser Himalaya. *Geological Magazine*, **124**, 323-345.

573 BRASIER, M.D., HEWITT, R. & BRASIER, C. 1978. On the late Precambrian-Early Cambrian
574 Hartshill Formation of Warwickshire. *Geological Magazine*, **115**, 21-36.
575 BRASIER, M.D., PEREJON, A. & DE SAN JOSE, M.A. 1979. Discovery of an important
576 fossiliferous Precambrian-Cambrian sequence in Spain. *Estudios Geológicos*, **35**, 379-
577 383
578 BRASIER, M.D., MAGARITZ, M., CORFIELD, R., HULIN, L., XICHE, W., LIN, O., ZHIWEN, J.,
579 HAMDI, B., TINGGUI, H. & FRASER, A. 1990. The carbon-and oxygen-isotope record of
580 the Precambrian–Cambrian boundary interval in China and Iran and their correlation.
581 *Geological Magazine*, **127**, 319-332.
582 BRASIER, M.D., ANDERSON, M.M.. & CORFIELD, R. 1992. Oxygen and carbon isotope
583 stratigraphy of early Cambrian carbonates in southeastern Newfoundland and
584 England. *Geological Magazine*, **129**, 265-279.
585 BRASIER, M.D., COWIE, J. & TAYLOR, M. 1994a. Decision on the Precambrian-Cambrian
586 boundary. *Episodes*, **17**, 95-100.
587 BRASIER, M.D., ROZHANOV, A.YU., ZHURAVLEV, A.YU., CORFIELD, R.M. & DERRY, L.A.
588 1994b. A carbon isotope reference scale for the Lower Cambrian succession in
589 Siberia: report of IGCP Project 303. *Geological Magazine*, **131**, 767-783.
590 BRASIER, M.D., SHIELDS, G., KULESHOV, V. & ZHEGALLO, E. 1996. Integrated chemo-and
591 biostratigraphic calibration of early animal evolution: Neoproterozoic–early Cambrian
592 of southwest Mongolia. *Geological Magazine*, **133**, 445-485.
593 BRASIER, M.D., GREEN, O.R. & SHIELDS, G.A. 1997. Ediacarian sponge spicule clusters from
594 southwestern Mongolia and the origins of the Cambrian fauna. *Geology*, **25**, 303-306.
595 BRASIER, M.D., MCCARRON, G., TUCKER, R., LEATHER, J., ALLEN, P. & SHIELDS, G.A. 2000.
596 New U-Pb zircon dates for the Neoproterozoic Ghubrah glaciation and for the top of
597 the Huqf Supergroup, Oman. *Geology*, **28**, 175-178.
598 BRASIER, M.D., CALLOW, R.H.T., MENON, L.R. & LIU, A.G. 2010. Osmotrophic Biofilms:
599 From Modern to Ancient. *In:* SECKBACH, J. & OREN, A. (eds) *Cellular Origin, Life in*
600 *Extreme Habitats and Astrobiology, Microbial Mats: Modern and Ancient*
601 *Microorganisms in Stratified Systems*. Springer Science+Business Media B.V.,
602 Dordrecht, 131-148.
603 BRASIER, M.D., ANTCLIFFE, J. B. & CALLOW, R.H.T. 2011. Evolutionary Trends in
604 Remarkable Fossil Preservation Across the Ediacaran-Cambrian Transition and the
605 Impact of Metazoan Mixing. *In* ALLISON, P.A. & BOTTJER, D.J. (eds) *Taphonomy:*

606 *Process and Bias Through Time*. Topics in Geobiology, Springer Science and
607 Business Media B.V., 519-567.
608 BRASIER, M.D., ANTCLIFFE, J.B. & LIU, A.G. 2012. The architecture of Ediacaran fronds.
609 *Palaeontology*, **55**, 1105-1124.
610 BRASIER, M.D., MCILROY, D., LIU, A.G., ANTCLIFFE, J.B. & MENON, L.R. 2013a. The oldest
611 evidence of bioturbation on Earth: Comment. *Geology*, **41**, e289.
612 BRASIER, M.D., LIU, A.G., MENON, L.R., MATTHEWS, J.J., MCILROY, D. & WACEY, D. 2013b.
613 Explaining the exceptional preservation of Ediacaran rangeomorphs from Spaniard's
614 Bay, Newfoundland: a hydraulic model. *Precambrian Research*, **231**, 122-135.
615 BUDD, G.E. & JENSEN, S. 2015. The origin of the animals and a 'Savannah'hypothesis for
616 early bilaterian evolution. *Biological Reviews*, doi: 10.1111/brv.12239.
617 BURKHARDT, F.H. & SMITH, S. (Eds) 1985. *The correspondence of Charles Darwin: Volume*
618 *1, 1821–1836*. Cambridge University Press, Cambridge, 752 p.
619 BUTTERFIELD, N.J. 2003. Exceptional fossil preservation and the Cambrian explosion.
620 *Integrated and Comparative Biology*, **43**, 166-177.
621 CALLOW, R.H.T. & BRASIER, M.D. 2009a. Remarkable preservation of microbial mats in
622 Neoproterozoic siliciclastic settings: implications for Ediacaran taphonomic models.
623 *Earth Science Reviews*, **96**, 207-219.
624 CALLOW, R.H.T. & BRASIER, M.D. 2009b. A solution to Darwin's dilemma of 1859:
625 exceptional preservation in Salter's material from the late Ediacaran Longmyndian
626 Supergroup, England. *Journal of the Geological Society, London*, **166**, 1-4.
627 CALLOW, R.H.T., MCILROY, D. & BRASIER, M.D. 2011. John Salter and the Ediacara Fauna
628 of the Longmyndian Supergroup. *Ichnos*, **18**, 176-187.
629 CALLOW, R.H.T., BRASIER, M.D. & MCILROY, D. 2013. Discussion: "Were the Ediacaran
630 siliciclastics of South Australia coastal or deep marine?" by Retallack et al.,
631 Sedimentology, 59, 1208-1236. *Sedimentology*, **60**, 2.
632 CARBONE, C. & NARBONNE, G.M. 2014. When life got smart: The evolution of behavioral
633 complexity through the Ediacaran and Early Cambrian of NW Canada. *Journal of*
634 *Paleontology*, **88**, 309-330.
635 CHEN, Z., ZHOU, C., MEYER, M., XIANG, K., SCHIFFBAUER, J.D., YUAN, X. & XIAO, S. 2013.
636 Trace fossil evidence for Ediacaran bilaterian animals with complex behaviours.
637 *Precambrian Research*, **224**, 690-701.
638 COBBOLD, E.S. 1900. The geology of Church Stretton. *In:* CAMPBELL, H.C.W. & COBBOLD,
639 E.S. (eds) *Church Stretton*. Wilding, Shrewsbury, 115 pp.

COCKS, L.R.M., MCKERROW, W.S. & VAN STAAL, C.R. 1997. The margins of Avalonia. *Geological Magazine*, **134**, 627-636.

DARWIN, C.R. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London, 502pp.

DUFOUR, S.C. & MCILROY, D. THIS VOLUME. Chemosynthesis and the ancestral feeding mode of early Ediacaran animals.

GEYER, G. & LANDING, A. THIS VOLUME. The Precambrian, Phanerozoic, and Ediacaran to Cambrian boundary: a historic approach to a long unresolved dilemma. *In:* BRASIER, A., MCILROY, D. & MCLOUGHLIN, N. (eds). Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier. ******, **-**.

GLAESSNER, M.F. 1984. *The dawn of animal life: a biohistorical study*. Cambridge University Press, Cambridge, 244 pp.

GOLD, D.A., RUNNEGAR, B., GEHLING, J.G. & JACOBS, D.K. 2015. Ancestral state reconstruction of ontogeny supports a bilaterian affinity for *Dickinsonia*. *Evolution & Development*, **17**, 315-324.

HERRINGSHAW, L. ET AL., THIS VOLUME. Engineering the explosion: the earliest bioturbators as ecosystem engineers. *In:* BRASIER, A., MCILROY, D. & MCLOUGHLIN N. (eds). Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier. **, **-**.

HOYAL CUTHILL, J.F. & CONWAY MORRIS, S. 2014. Fractal branching organizations of Ediacaran rangeomorph fronds reveal a lost Proterozoic body plan. *Proceedings of the National Academy of Sciences*, **111**, 13122-13126.

HSU, K.J., OBERHAENSLI, H., GAO, Y., SUN, S., CHEN, H. & KRAHENBUHL, U. 1985. "Strangelove ocean" before the Cambrian explosion. *Nature*, **316**, 809-811.

IVANTSOV, A.Yu. 2016. Reconstruction of *Charniodiscus yorgensis* (macrobiota from the Vendian of the White Sea). *Paleontological Journal*, **50**, 1-12.

KILNER, B., MAC NIOCAILL, C. & BRASIER, M.D. 2005. Low-latitude glaciation in the Neoproterozoic of Oman. *Geology*, **33**, 413-416.

KNOLL, A.H., HAYES, J.M., KAUFMAN, A.J., SWETT, K. & LAMBERT, I.B. 1986. Secular variations in carbon isotope ratios from Upper Proterozoic successions of Svalbard and East Greenland. *Nature*, **321,** 832-838. (1986)

KNOLL, A.H., KAUFMAN, A.J., SEMIKHATOV, M.A., GROTZINGER, J.P. & ADAMS, W. 1995. Sizing up the sub-Tommotian unconformity in Siberia. *Geology*, **23**, 1139-1143.

KOLESNIKOV, A.V., GRAZDHANKIN, D.V. & MASLOV, A.V. 2012. Arumberia-type structures in the Upper Vendian of the Urals. *Doklady Earth Sciences*, **447**, 1233-1239.

KOLESNIKOV, A.V., MARUSIN, V.V., NAGOVITSIN, K.E., MASLOV, A.V. & GRAZHDANKIN, D.V. 2015. Ediacaran biota in the aftermath of the Kotlinian Crisis: Asha Group of the South Urals. *Precambrian Research*, **263**, 59-78.

LAFLAMME, M., SCHIFFBAUER, J.D. & NARBONNE, G.M. 2011. Deep-water microbially induced sedimentary structures (MISS) in deep time: the Ediacaran fossil *Ivesheadia*. *In:* NOFFKE, N. & CHAFETZ, H. (eds) *Microbial mats in siliciclastic depositional systems through time*. SEPM (Society for Sedimentary Geology) Special Publication, **101**, 111-123.

LANDING, E., GEYER, G., BRASIER, M. D., & BOWRING, S. A. 2013. Cambrian evolutionary radiation: context, correlation, and chronostratigraphy—overcoming deficiencies of the first appearance datum (FAD) concept. *Earth Science Reviews*, **123**, 133-172.

LANDING, E. & GEYER, G. THIS VOLUME, Title tbc. *In:* BRASIER, A., MCILROY, D. & MCLOUGHLIN N. (eds). Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier. **, **-**.

LEATHER, J., ALLEN, P.A., BRASIER, M.D. & COZZI, A. 2002. Neoproterozoic snowball Earth under scrutiny: evidence from the Fiq glaciation of Oman. *Geology*, **30**, 891-894.

LINDSAY, J.F., KRUSE, P.D., GREEN, O.R., HAWKINS, E., BRASIER, M.D., CARTLIDGE, J. & CORFIELD, R. M. 2005. The Neoproterozoic–Cambrian record in Australia: a stable isotope study. *Precambrian Research*, **143**, 113-133.

LIU, A.G. 2016. Framboidal pyrite shroud confirms the 'death mask'model for moldic preservation of Ediacaran soft-bodied organisms. *PALAIOS*, **31**, 259-274.

LIU, A.G. & BRASIER, M.D. 2012. A Global Comparative Analysis of Ediacaran fossil localities. Oxford, 130 pp.

LIU, A.G. & MCILROY, D. 2015. Horizontal surface traces from the Fermeuse Formation, Ferryland (Newfoundland, Canada), and their place within the late Ediacaran ichnological revolution. *In:* MCILROY, D. (ed.) *Ichnology*. Geological Association of Canada Miscellaneous Publications, **9**, 141-156.

LIU, A.G., MCILROY, D. & BRASIER, M.D. 2010a. First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland. *Geology*, **38**, 123-126.

LIU, A.G., MCILROY, D. & BRASIER, M.D. 2010b. First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland: Reply. *Geology*, **38**, e224.

LIU, A.G., MCILROY, D., ANTCLIFFE, J.B. & BRASIER, M.D. 2011. Effaced preservation in the Ediacaran biota of Avalonia and its implications for the early macrofossil record. *Palaeontology*, **54**, 607-630.

LIU, A.G., MCILROY, D., MATTHEWS, J.J. & BRASIER, M.D. 2012. A new assemblage of juvenile Ediacaran fronds from the Drook Formation, Newfoundland. *Journal of the Geological Society, London*, **169**, 395-403.

LIU A.G., BRASIER, M.D., BOGOLEPOVA, O.K., RAEVSKAYA, E.G. & GUBANOV, A.P. 2013. First report of a newly discovered Ediacaran biota from the Irkineeva Uplift, East Siberia. *Newsletters on Stratigraphy*, **46**, 95-110.

LIU, A.G., MATTHEWS, J.J., MCILROY, D. & BRASIER, M.D. 2014a. Confirming the metazoan character of a 565 Ma trace-fossil assemblage from Mistaken Point, Newfoundland. *PALAIOS*, **29**, 420-430.

LIU, A.G., MATTHEWS, J.J., MENON, L.R., MCILROY, D. & BRASIER, M.D. 2014b. *Haootia quadriformis* n. gen., n. sp., interpreted as a muscular cnidarian impression from the Late Ediacaran period (approx. 560 Ma). *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141202.

LIU, A.G., KENCHINGTON, C.G. & MITCHELL, E.G. 2015a. Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. *Gondwana Research*, **27**, 1355-1380.

LIU, A.G., MATTHEWS, J.J., MENON, L.R., MCILROY, D. & BRASIER, M.D. 2015b. The arrangement of possible muscle fibres in the Ediacaran taxon *Haootia quadriformis. Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20142949.

LIU, A.G., MATTHEWS, J.J., & MCILROY, D. 2016. The *Beothukis*/*Culmofrons* problem and its bearing on Ediacaran macrofossil taxonomy: evidence from an exceptional new fossil locality. *Palaeontology*, **59**, 45-58.

MACDONALD, F.A., PRUSS, S.B. & STRAUSS, J.V. 2014. Trace fossils with spreiten from the Late Ediacaran Nama Group, Namibia: Complex feeding patterns five million years before the Precambrian–Cambrian boundary. *Journal of Paleontology*, **88**, 299-308.

MAGARITZ, M., HOLSER, W.T. & KIRSCHVINK, J.L. 1986. Carbon-isotope events across the Precambrian/Cambrian boundary on the Siberian Platform. *Nature*, **320,** 258-259.

MCILROY, D. & BRASIER, M.D. THIS VOLUME. Possible in-vivo frond-sediment interactions of an unknown frondose taxon from Mistaken Point, Newfoundland.

MCILROY, D. & WALTER, M.R. 1997. A reconsideration of the biogenicity of *Arumberia banksi* Glaessner & Walter. *Alcheringa*, **21**, 79-80.

MCILROY, D., BRASIER, M.D. & LANG, A.S. 2009. Smothering of microbial mats by macrobiota: implications for the Ediacara biota. *Journal of the Geological Society, London*, **166**, 1117-1121.

MCILROY, D., BRASIER, M.D. & MOSELEY, J.B. 1998. The Proterozoic-Cambrian transition within the 'Charnian Supergroup' of central England and the antiquity of the Ediacara fauna. *Journal of the Geological Society, London*, **155**, 401-411.

MCILROY, D., CRIMES, T.P. & PAULEY, J.C. 2005. Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, U.K. *Geological Magazine*, **142**, 441-455.

MCKERROW, W.S., SCOTESE, C.R. & BRASIER, M.D. 1992. Early Cambrian continental reconstructions. *Journal of the Geological Society*, **149**, 599-606.

MENON, L.R., MCILROY, D. & BRASIER, M.D. 2013. Evidence for Cnidaria-like behavior in ca. 560 Ma Ediacaran *Aspidella*. *Geology*, **41**, 895-898.

MENON, L.R., MCILROY, D., LIU, A.G. & BRASIER, M.D. 2016. The dynamic influence of microbial mats on sediments: fluid escape and pseudofossil formation in the Ediacaran Longmyndian Supergroup, UK. *Journal of the Geological Society, London*, **173**, 177-185.

MENON, L. BRASIER, M.D., & MCILROY, D. THIS VOLUME. *Intrites* from the Longmyndian of Shropshire, UK reinterpreted as a new form of MISS.

MOOR, R., 2016. *On Trails*. Simon & Schuster, New York. 337 pp.

NARBONNE, G.M., LAFLAMME, M., GREENTREE, C. & TRUSLER, P., 2009. Reconstructing a lost world: Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland. *Journal of Paleontology*, **83**, 503-523.

NARBONNE, G.M., XIAO, S. & SHIELDS, G.A. 2012. The Ediacaran Period. *In:* GRADSTEIN, F.M., OGG, J., SCHMIDT, M. & OGG, G. (eds) *The Geologic Time Scale 2012*. Elsevier Science Limited, 413-436.

NOBLE, S.R., CONDON, D.J., CARNEY, J.N., WILBY, P.R., PHARAOH, T.C. & FORD, T.D. 2015. U-Pb geochronology and global context of the Charnian Supergroup, UK: constraints on the age of key Ediacaran fossil assemblages. *Geological Society of America Bulletin*, **127**, 250-265.

PEAT, C. 1984. Precambrian microfossils from the Longmyndian of Shropshire. *Proceedings of the Geologist's Association*, **5**, 17-22.

PETERS, S.E. & GAINES, R.R. 2012. Formation of the "Great Unconformity" as a trigger for the Cambrian explosion. *Nature*, **484**, 363-366.

RETALLACK, G.J. 1994. Were the Ediacaran Fossils Lichens? *Paleobiology*, **20**, 523-544.

RETALLACK, G.J. 2010. First evidence for locomotion in the Ediacara biota from the 565Ma Mistaken Point Formation, Newfoundland: Comment. *Geology*, **38**, e223.

RETALLACK, G.J. 2013. Ediacaran life on land. *Nature*, **493**, 89-92.

SALTER, J.W. 1856. On fossil remains in the Cambrian rocks of the Longmynd and North Wales. *Quarterly Journal of the Geological Society*, **12**, 246-251.

SALTER, J.W. 1857. On annelide burrows and surface markings from the Cambrian rocks of the Longmynd. *Quarterly Journal of the Geological Society*, **13**, 199-207.

SEILACHER, A. 1984. Late Precambrian and Early Cambrian Metazoa: preservational or real extinctions? *In:* HOLLAND, H.D. & TRENDALL, A.F. (eds) *Patterns of change in earth evolution*, Springer, Berlin Heidelberg, pp. 159-168.

SEILACHER, A. 1989. Vendozoa: organismal construction in the Proterozoic biosphere. *Lethaia*, **22**, 229-239.

SHIELDS, G., STILLE, P., BRASIER, M.D. & ATUDOREI, N.-V. 1997. Stratified oceans and oxygenation of the late Precambrian environment: a post glacial geochemical record from the Neoproterozoic of W. Mongolia. *Terra Nova*, **9**, 218-222.

SHIELDS-ZHOU, G.A., HILL, A.C. & MACGABHANN, B.A. 2012. The Cryogenian Period. *In:* GRADSTEIN, F.M., OGG, J., SCHMIDT, M. & OGG, G. (eds) *The Geologic Time Scale 2012*. Elsevier Science Limited, 393-412.

TIMOFEYEV, B.V., CHOUBERT, G. & FAURE-MURET, A. 1980. Acritarchs of the Precambrian in mobile zones. *Earth Science Reviews*, **16**, 249-255.

TOGHILL, P. 2006. *Geology of Shropshire*. The Crowood Press Ltd, Marlborough, 256 pp.

TORSVIK, T.H., SMETHURST, M.A., MEERT, J.G., VAN DER VOO, R., MCKERROW, W.S., BRASIER, M.D., STURT, B.A. & WALDERHAUG, H.J. 1996. Continental break-up and collision in the Neoproterozoic and Palaeozoic—a tale of Baltica and Laurentia. *Earth-Science Reviews*, **40**, 229-258.

TUCKER, 1986. Carbon isotope excursions in Precambrian/Cambrian boundary beds, Morocco. *Nature*, **319**, 48-50.

TUCKER, 1992. The Precambrian-Cambrian boundary: Seawater chemistry, ocean circulation, and nutrient supply in metazoan evolution, extinction, and biological mineralization. *Journal of the Geological Society, London*, **149**, 655-668.

WACEY, D., MCLOUGHLIN, N., STOAKES, C.A., KILBURN, M.R., GREEN, O.R. & BRASIER, M.D. 2010. The 3426-3350 Ma Strelley Pool Formation in the East Strelley greenstone belt – a field and petrographic guide. *Geological Survey of Western Australia Record* 2010/10.

WACEY, D., KILBURN, M.R., SAUNDERS, M., CLIFF, J.B., KONG, C., LIU, A.G., MATTHEWS, J.J. & BRASIER, M.D. 2015. Uncovering framboidal pyrite biogenicity using nano-scale CN_{org} mapping. *Geology*, **43**, 27-30.

WILBY, P.R., CARNEY, J.N. & HOWE, M.P.A. 2011. A rich Ediacaran assemblage from eastern Avalonia: evidence of early widespread diversity in the deep ocean. *Geology*, **39**, 655-658.

WILBY, P.R., KENCHINGTON, C.G. & WILBY, R.L. 2015. Role of low intensity environmental disturbance in structuring the earliest (Ediacaran) macrobenthic tiered communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **434**, 14-27.

ZHOU, C., BRASIER, M.D. & XUE, Y. 2001. Three-dimensional phosphatic preservation of giant acritarchs from the terminal Proterozoic Doushantuo Formation in Guizhou and Hubei Provinces, South China. *Palaeontology*, **44**, 1157-1178.

Figure captions

Fig. 1 Martin Brasier in Newfoundland. (**a**) On the 'E' Surface at Mistaken Point, in his socks, 2005. (**b**) Sketching on the Bonavista Peninsula, 2008. Photo credit: Jack Matthews.

Fig. 2 (**a**) Martin (inset) undertaking laser scanning in the field, Memorial Crags, Charnwood Forest, Leicestershire. (**b**) An example of a laser-generated digital image: the holotype of *Charnia masoni* (see Brasier & Antcliffe 2009).

834 **Fig. 3** Martin's method of drawing Ediacaran fossils, as exemplified by his work on the
835 holotype of *Charniodiscus concentricus*, from Charnwood Forest, Leicestershire. (**a**)
836 Photograph of a cast of the holotype specimen in New Walk Museum, Leicester, image
837 courtesy of the British Geological Survey. (**b**) Martin's sketch of the key features of the
838 specimen, developed via drawings made from photographs and laser scan data. (**c**) Martin's
839 novel interpretation of multiple fronds emanating from the stem of the organism.

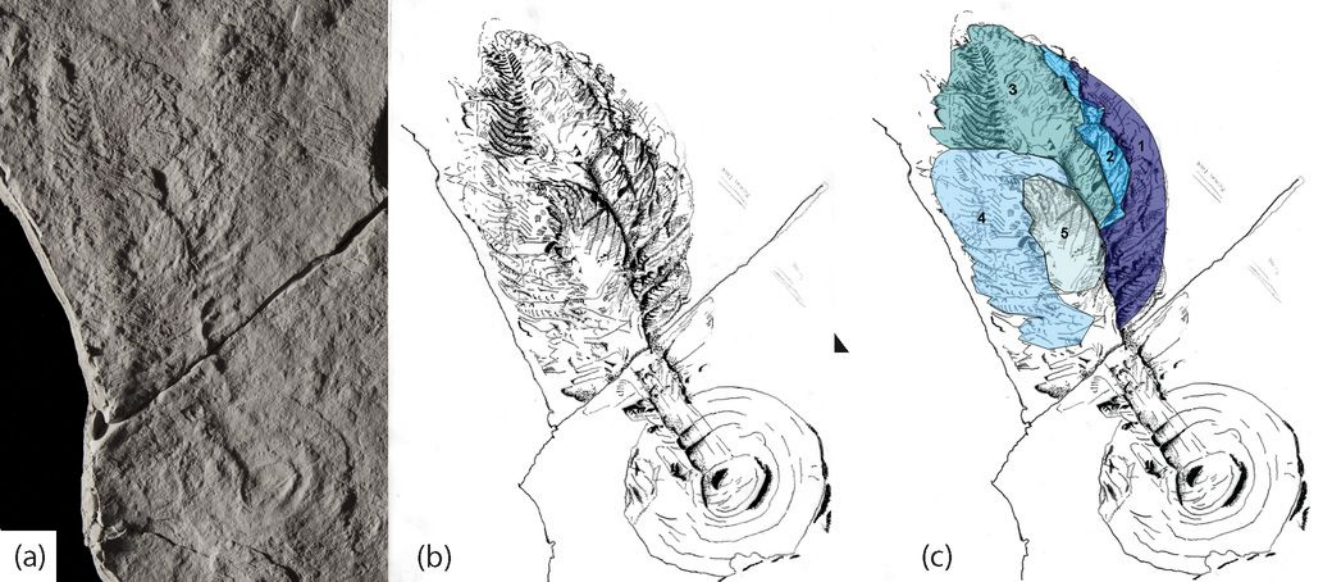
840

841 **Fig. 4** Excerpt from one of Martin's (many) field notebooks, showing a log drawn through
842 the fossil-bearing section at Spaniard's Bay, Newfoundland (work that was eventually
843 published in Brasier *et al*. 2013b).

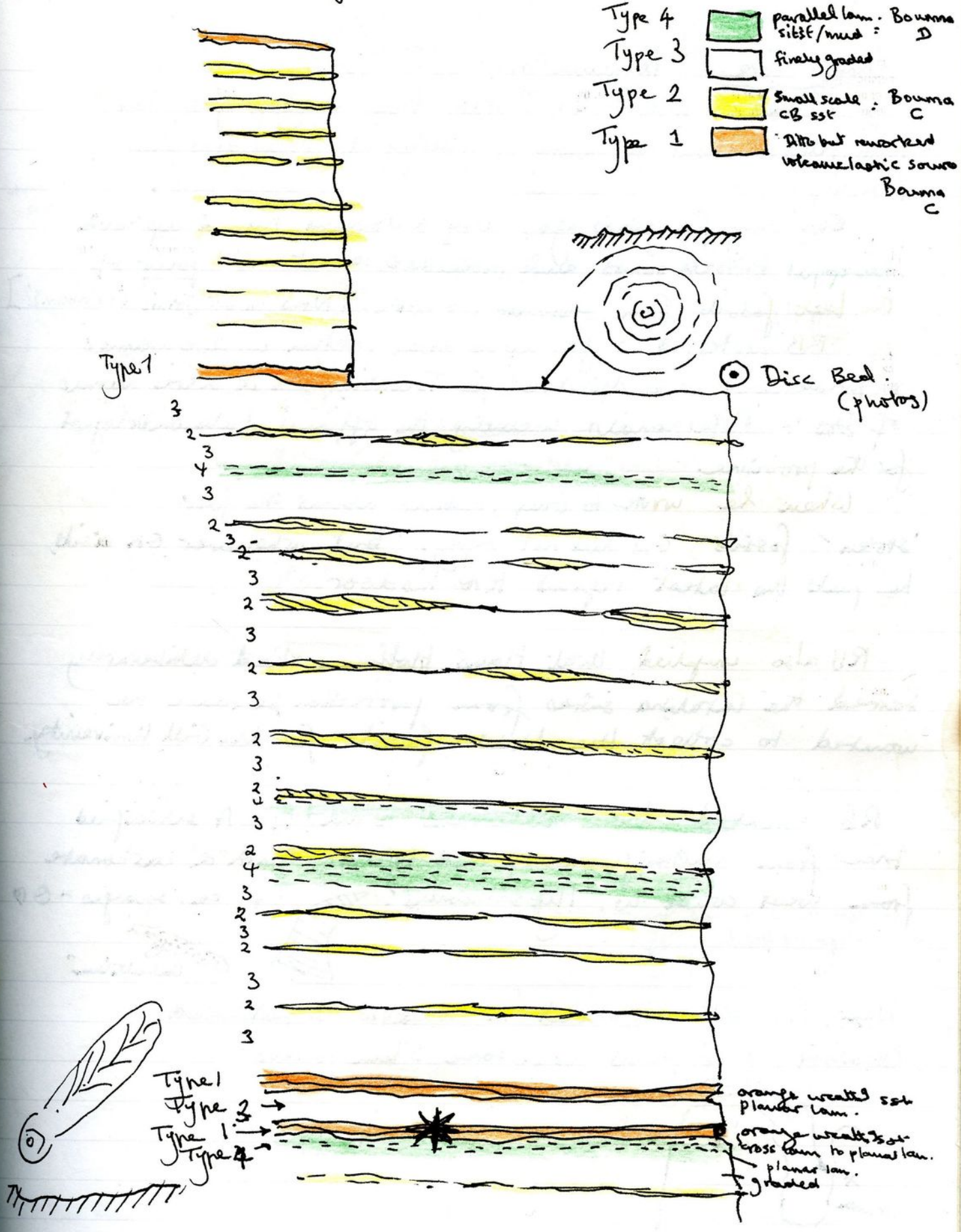

(a)


(b)


(a)
(b)
GS200


(a)
(b)
(c)
1
2
3
4
5

x 0.5 [illegible] section through 2 fossil beds (photos)



* = Main fossil bed